EMBRYOLOGICAL DEVELOPMENT OF INBRED AND HYBRID ZEA MAYS L.

By

Fu-Hsiung Wang

B.S., National Tsing Hua University, 1936
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THESIS

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EMBRYOLOGICAL DEVELOPMENT OF INBRED AND HYBRID ZEA MAYS L. [1]

F. H. Wang[2]

The early researches in maize genetics before the rediscovery of Mendel's laws have been reviewed by Singleton (1935). The early literature on hybrid vigor has been discussed by Jones (1918) and development of hybrid corn in relation to heterosis has been summarized by Singleton (1941). The problem of heterosis has been critically reviewed by East (1936) and more recently by Whaley (1944), so that only a few ideas most pertinent to the present problem need be mentioned.

Shull (1908, 1909, 1910, 1911) was the first to attempt to give a genetic explanation of hybrid vigor in maize. He introduced the term "heterozygosis," from which "heterosis" was derived. Almost at the same time East (1908, 1909), who was also working on maize, contributed to knowledge of the genetic nature of hybridization. Bruce (1910) believed that hybrid vigor is the result of the number of "dominant" genes rather than of the "heterozygous" genes present in the hybrid, as Shull (1908) visualized. Keeble and Pellew (1910) reached the same conclusion as Bruce, while East and Hayes (1912) and Shull (1914) concluded that the stimulus to development through hybridization is directly derived from heterozygosity. Later Jones (1917) suggested "the dominance of linked genes hypothesis" based on the idea of dominant favorable genes of Bruce (1910), Keeble and Pellew (1910) and Morgan's (1915) discovery of linkage. Up to 1930 Jones' theory for the explanation of heterosis had been generally accepted.

In 1930 Ashby (1930, 1932, 1936) began to publish a series of physiological investigations on the immediate cause of hybrid vigor. He studied the growth rate of inbred and hybrid seedlings in maize for a period of 20–70 days after germination of the seeds and found no difference in the rate of growth. Ashby concluded that hybrid vigor is due to the difference in initial embryo size—the so-called "initial capital hypothesis." He further said that the growth rate in his plants seemed to be determined by a single gene. In a second series of Ashby's (1937) and in Luckwill's (1937) studies dealing with hybrid vigor in tomatoes the same conclusion was reached, but modified the concept of "original capital" to apply to the axis of the embryo rather than the embryo as a whole. East (1936) criticized Ashby's work in many details. Lindstrom (1935) failed to substantiate Ashby's thesis as his experimental results showed that decapitated vigorous F_1 maize hybrid seedlings, deprived of some of the "capital," still exceeded the parental strains in dry weight at maturity. Sprague (1936) and Murdoch (1940) studied the weights of embryo axes of maize. Sprague concluded that "hybrid vigor can not be attributed to the maintenance of an initial difference in embryo size," while Murdoch found that the embryo axes of the two hybrids were significantly heavier than those of their parents. Whaley (1939) made extensive studies in tomatoes and concluded that "the presence of the heterosis is not always accompanied in the hybrid by a larger embryo" and "no relation was found, either in the embryo or during development, between the volume of the apical meristem and heterosis." Shafer (1944), in his studies of the relation of embryo axis weights to heterosis, reported: "some hybrids grow at a much faster rate than either parent" and "some hybrids show heterosis in spite of having embryo axes no heavier than those of their parents."

More recently Buchholz (1945) found that the growth rate of hybrid pine embryos is greater than that of the selfed embryos of the parents and that there is no difference in embryo size or meristem size at comparable morphological stages. The purpose of the present investigation was to study the growth rate of the embryo and endosperm of inbred and hybrid maize during the period between fertilization and the maturing of the seed and its relation to heterosis.

Randolph (1936) studied the developmental morphology of the caryopsis in maize based upon the observations of the sectioned slides of the dent variety Pride of Michigan. Copeland (1940) published an abstract in which he pointed out that some hybrid maize embryos showed added vigor at the 4–10 day stages. Even before Ashby, Kiesselbach (1926) in his studies of the immediate effect of gametic relationship and of parental type upon the kernel weight of corn reported that "nineteen inbred strains of two varieties whose kernel weights were increased an average of 10.1 per cent by cross-pollination in 1923 had their embryos, endosperms, and pericarps increased 11.8, 10.4, and 3.2 per cent, respectively." However, the growth rate of inbred and hybrid maize for the period between fertilization and the maturing of the seed is still not known.

Material and methods.—The plants for this investigation were grown at the University Experimental Farm. Three well-established inbred lines were used for experiments: two yellow lines, 38–11 and WF9, and one white line, K–64. The inbred lines were recommended by Professor C. M. Woodworth, Agronomist, and were so chosen because they are being widely used in breeding commercial hybrid corn. The ears of eight to ten plants in each line were bagged as usual before silking. Just before pollination the group of silks was carefully separated into two halves; the separation into right and

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The author wishes to express his sincere appreciation to Professor J. T. Buchholz, under whose direction this work was initiated and carried out. He is also grateful to Professor C. M. Woodworth of the University of Illinois for his kind help in offering the use of experimental material.

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left halves was begun with a needle, and the two strands of silks were covered with separate shoot bags. These shoot bags, which were small, were perforated at the inner side around the silks to enclose and isolate them permanently. These smaller bags were fastened together and held in place by Scotch tape at the top. All the tassels of the plants in the vicinity were bagged during the operation in order to avoid possible contamination and shoots were kept covered with larger bags except during pollination. The pollen from several plants of one line was collected, thoroughly mixed, cleaned with soil sieves and then applied to the silks at the right side of the ear of its own line for sib-selfing and to those at the left side of the ear of another line for hybridization. After one kind of pollen was used, the instruments and the hands were sterilized and a clean sieve was used. Then followed work with the pollen from the other line, so that all pollinations were completed within a few hours.

The time interval in days for collections in each series is listed as follows:

Series I, crosses between 38–11 and WF9 (pollinated on August 12, 1945): 8, 10, 12, 16, 20, 25 and 44 days.

Series II, crosses between 38–11 and WF9 (pollinated on August 16, 1945): 8, 10, 12, 14, 17, 21, 25, 40 and 60 (mature) days.

Series III, crosses between 38–11 and K–64 (pollinated on August 16, 1945): 8, 10, 14, 20, 25, 40 and 60 (mature) days.

The seeds were fixed in formalin-acetic-alcohol solution or the entire ear was fixed for later dissection. The seeds on both ends and the doubtful seeds on the margins between hybrid and selfed halves were not used. In the early stages the hybrid and selfed seeds were identified by the position on the ear. Tracing of the wilted silks, while they still remained in the separate bags, down to the kernels, and also tracing of the marginal kernels, which were sterile as a result of injury to the silks in separating them, helped to ascertain the origin of the seed. During the more advanced stages the color of plumule and that of the endosperm became dis-

TABLE 1. *Measurements of embryo and endosperm of 38–11 and WF9 and their reciprocal hybrids (pollinated on August 12, 1945).*

Days from pollination	Heritage	Measurements[a] Embryo (A) W N	W M	L N	L M	V N	V M	Dw N	Dw M	Endosperm (B) V N	V M	Dw N	Dw M	A × 100[b] / A + B V	A × 100[b] / A + B Dw
8	38–11	50	458	50	439	..	...	..	....	50	4.2	50	0.14	....	....
	38–11 × WF9	50	474	50	438	..	...	..	....	50	5.0	50	0.17	....	....
	WF9 × 38–11	50	331	50	334	..	...	..	....	50	2.8	50	0.074	....	....
	WF9	50	317	50	296	..	...	..	....	50	2.0	50	0.074	....	....
10	38–11	50	1074	50	1317	..	...	..	....	50	17.2	50	0.80	....	....
	38–11 × WF9	50	1352	50	1697	..	...	..	....	50	27.0	50	1.06	....	....
	WF9 × 38–11	50	1302	50	1574	..	...	..	....	50	26.2	50	0.73	....	....
	WF9	50	1134	50	1274	..	...	..	....	50	20.0	50	0.62	....	....
12	38–11	50	1492	50	1920	..	. .	..	....	50	35.6	50	2.47	....	....
	38–11 × WF9	50	1613	50	2115	..	...	..	....	50	37.0	50	2.79	....	....
	WF9 × 38–11	50	1614	50	2129	..	. .	..	....	50	43.4	50	1.62	....	....
	WF9	50	1550	50	1948	..	...	..	....	50	42.6	50	1.59	....	....
16	38–11	54	1790	54	2648	50	1.6	50	0.30	40	63	50	15.6	2.46	1.99
	38–11 × WF9	49	2152	49	3407	50	3.0	50	0.68	40	80	40	20.3	3.62	3.24
	WF9 × 38–11	50	2006	50	3096	50	2.4	50	0.48	50	102	50	13.7	2.30	3.39
	WF9	50	1833	50	2623	50	1.8	50	0.26	50	96	50	8.7	1.84	2.90
20	38–11	50	2597	50	3820	50	6.0	50	1.75	50	114	50	43.06	5.00	3.69
	38–11 × WF9	50	2930	50	4662	50	8.8	50	2.94	50	144	50	49.28	5.76	5.63
	WF9 × 38–11	50	2704	50	4063	50	6.2	50	2.23	60	166	60	46.64	3.60	4.56
	WF9	53	2730	53	3690	50	5.6	50	1.81	50	162	50	39.06	3.34	4.43
25	38–11	53	3605	53	5515	50	13.6	50	5.76	50	162	50	77.6	7.74	6.89
	38–11 × WF9	63	4137	63	6498	50	18.2	50	8.43	50	174	50	86.6	9.46	8.87
	WF9 × 38–11	72	3526	72	5680	50	15.4	50	5.20	50	212	50	77.3	6.76	6.30
	WF9	64	3735	64	5400	50	12.8	50	4.49	50	194	50	64.4	6.19	6.52
44	38–11	50	4205	50	6757	50	32.4	49	19.08	50	248	50	178.9	11.5	9.64
	38–11 × WF9	50	5015	50	8325	50	45.4	50	26.64	50	314	50	214.2	12.7	11.04
	WF9 × 38–11	50	4036	50	7977	50	43.8	49	19.94	50	262	50	184.6	14.3	9.75
	WF9	50	4163	50	7612	50	43.8	50	20.40	50	244	50	171.0	15.2	10.65

[a] Symbols: W = Width in microns. L = Length in microns. V = Volume in mm^3. Dw = Dry weight in mg. N = Number (Frequency). M = Mean.

[b] $\frac{A \times 100}{A + B}$ = Embryo in percentage of the embryo sac.

tinctive characters which could be used to distinguish hybrid seeds from selfed seeds.

Usually fifty embryos and the same number of endosperms of each sample were dissected under the binocular microscope. The embryos were individually measured in maximum width and maximum length with the ocular micrometer under the microscope.

The total volume of the embryo and that of the endosperm were obtained by water or dilute alcohol displacement as measured in different sizes of calibrated tubes. The mean value was obtained by dividing the total volume by the number used in each sample. The volume of the youngest embryos that were measured was obtained by the use of a special instrument made of a mechanical stage with vernier and a calibrated glass tube fastened to a stand with a clamp, as designed by Professor J. T. Buchholz. This instrument gives the measurement accurately to 2.6 mm^3.

The dry weight of each sample was determined. The embryos and the endosperms were dried in an oven of 70°±C. for 3 hours to overnight. All the data were tabulated in three tables (tables 1, 2, and 3). By plotting the mean values of various measurements—width, length, volume, etc.—against the time after pollination, a series of growth curves was obtained. The observations during the early stages in development were plotted in semi-logarithmic graphs in order to show the difference of the small values.

Before analysis of the data concerning embryo volume, two technical difficulties in measurement should be described. First, when the young embryos were removed from the fixative and spread over the blotting paper, the degree of dryness of the surface of the embryos greatly influenced the accuracy of the measurements, regardless of the shrinkage caused by the fixative and no matter how accurately it is possible to read the volume of liquid displacement. Secondly, handling of the small embryos is difficult. In order to obtain the greatest possible accuracy a small glass capillary tube was used. The embryos have to be transferred one by one. Once the embryo clings to the side of the tube, it will carry down some liquid adhering to the walls when pushed into the liquid. Since the young embryo does not sink in water, dilute alcohol has to be used. If the procedure takes too long, a considerable amount of alcohol will have evaporated. Due to these technical difficulties, the early collections, younger than 12 days, were not measured. Even in those early stages that were measured, great experimental error may be expected.

A REVIEW OF MORPHOLOGICAL DEVELOPMENT OF THE MAIZE EMBRYO.—The time interval between pollination and fertilization in maize varies with two factors: temperature and length of the silk. No observations bearing on the period of pollen tube growth were made. The interval is generally 16–24 hours under ordinary field conditions, according to Randolph (1936).

My own observations combined with those of Randolph (1936) show that the development of embryos in maize may be divided into the following stages:

Cell division (2–7 days). The young embryo is undifferentiated except that cell division is more active in the apical region. No definite boundary is found between the embryo proper and the suspensor.

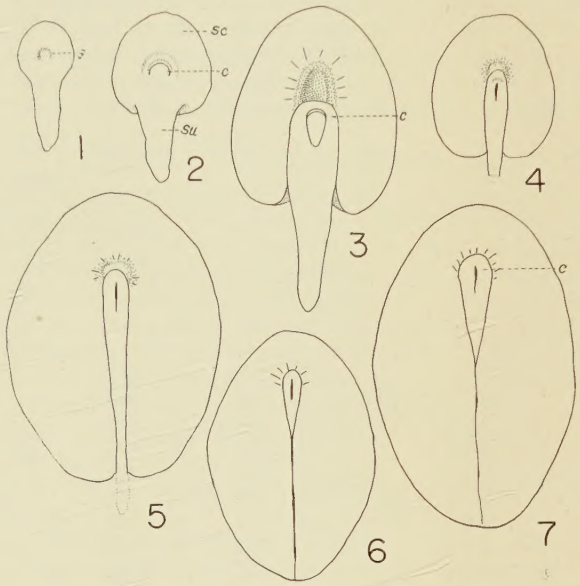

Fig. 1–7. Outline drawings of maize embryos of 38–11, 8 to 40 days after pollination, showing changes in shape and size and external structures: Fig. 1–3, stages at 8, 10 and 12 days, showing differentiation of stem tip primordium, coleoptile primordium, scutellum and suspensor; S, stem tip primordium; Sc, scutellum; C, coleoptile primordium; Su, suspensor; ×24. Fig. 4 and 5, stages at 14, 17 and 21 days; ×12. Fig. 6 and 7, stages at 25 and 40 days; ×7. See text for further description.

The differentiation of axis (8–10 days). This stage begins with the formation of epidermis. The differentiation of stem and root meristems follows the formation of scutellum. The activity of cell division shifts to the newly formed plumule-radicle axis. Considerable growth of suspensor continues (fig. 1 and 2).

The differentiation of leaf primordia (10–20 days). This period includes the formation of primordia of the coleoptile which is still open in fig. 3, closes to a slit-opening in later stages (fig. 4–7). This stage also includes formation of the first seedling leaves. These are accompanied by a remarkable growth of the scutellum which is beginning to ensheath the plumule-radicle axis (fig. 3, 4 and 5). The suspensor ceases to grow toward the end of this stage and gradually loses its function.

Growth and continued internal differentiation (20–45 days). The primordia of additional seedling leaves are formed. This stage also includes differentiation of procambium strands of the vas-

cular system and general growth of all structures with the result that the embryo is morphologically mature in about 45 days. The external appearance is shown in fig. 6 and 7.

Maturation (45 days-maturity). No new organ develops during this last period. Further growth is limited to the maturation and full development of the structures found in the mature embryo.

INVESTIGATIONS.—*Embryo development of the inbred and hybrid maize.*—Embryo development in width.—Series I, crosses between 38–11 and WF9 (pollinated on August 12, 1945).—The embryo already shows a definite difference in width in the first collection made 8 days after pollination. The inbred line 38–11 is in a more advanced stage than that of inbred line WF9 up to this date. Both hybrids stand a little higher in comparison with their respective maternal parents. Two days later, however, the hybrid WF9 × 38–11 exceeds both parents in width until the time between 16 and 20 days, then slows down again and finally drops below the parents toward the end of the observations, 44 days after pollination shown in table 1. On the other hand, the inbred parent WF9 exceeds the inbred parent 38–11 in width but it is again a little below in width at the last observation. The fast growing hybrid 38–11 × WF9 maintains its leading position in embryo width throughout the period of observation.

TABLE 2. *Measurements of embryo and endosperm of 38–11 and WF9 and their reciprocal hybrids (pollinated on August 16, 1945).*

Days from pollination	Heritage	Measurements[a] Embryo (A) W N	W M	L N	L M	V N	V M	Dw N	Dw M	Endosperm (B) V N	V M	Dw N	Dw M	A × 100[b] / A + B V	A × 100[b] / A + B Dw
8	38–11	50	508	50	489	..	....	..	....	50	5.4	50	0.136	...	...
	38–11 × WF9	50	544	50	513	..	....	..	....	50	5.6	50	0.162	...	...
	WF9 × 38–11	33	302	33	288	..	....	..	....	33	3.3	33	0.073	...	...
	WF9	34	243	34	220	..	....	..	....	34	2.6	34	0.056	...	...
10	38–11	50	829	50	872	..	....	..	....	50	12.2	50	0.312	...	...
	38–11 × WF9	50	920	50	990	..	....	..	....	50	14.4	50	0.400	...	...
	WF9 × 38–11	40	771	40	778	..	....	..	....	40	8.0	40	0.255	...	...
	WF9	40	664	40	640	..	....	..	....	40	8.0	40	0.212	...	...
12	38–11	50	966	50	1235	50	0.08	50	0.014	50	26.0	50	1.544	0.30	0.89
	38–11 × WF9	50	1098	50	1428	50	0.13	50	0.026	50	33.6	50	1.940	0.38	1.23
	WF9 × 38–11	50	1285	50	1528	44	0.29	44	0.009	50	21.2	50	0.664	1.35	1.34
	WF9	50	1248	50	1386	50	0.16	37	0.007	50	20.0	50	0.580	0.79	1.19
14	38–11	50	1346	50	1737	50	0.27	50	0.062	50	38	48	4.281	0.71	1.43
	38–11 × WF9	50	1558	50	2250	50	0.46	49	0.106	50	48	50	5.700	0.95	1.83
	WF9 × 38–11	50	1818	50	2586	50	0.70	47	0.193	50	78	50	9.800	0.87	1.93
	WF9	50	1697	50	2231	50	0.64	49	0.147	50	64.8	50	6.350	0.97	2.26
17	38–11	50	2221	50	3132	50	2.29	50	0.608	50	76	50	19.126	2.93	3.89
	38–11 × WF9	50	2608	50	3915	50	3.43	50	1.061	50	96	50	24.728	3.45	4.11
	WF9 × 38–11	50	2536	50	3726	50	2.70	50	0.860	50	128	50	25.508	2.06	3.26
	WF9	50	2434	50	3421	50	2.10	50	0.696	50	114	50	18.488	1.83	3.63
21	38–11	109	2958	109	4357	50	6.24	109	2.525	50	106	50	44.83	5.56	5.34
	38–11 × WF9	113	3459	113	5407	50	9.57	113	4.079	50	126	50	48.74	7.08	7.72
	WF9 × 38–11	50	3180	50	4873	50	7.70	50	3.216	50	154	50	55.56	4.76	5.47
	WF9	50	3407	50	4598	50	6.60	50	2.740	50	152	50	47.94	4.16	5.40
25	38–11	50	3356	50	5173	50	12.8	49	5.877	50	138	50	77.65	8.48	7.04
	38–11 × WF9	50	3740	50	5903	50	15.8	50	7.536	50	150	50	80.80	9.53	8.53
	WF9 × 38–11	57	3697	57	6287	50	14.5	56	6.932	50	222	50	92.72	6.13	6.96
	WF9	44	4096	44	6084	44	13.8	43	6.686	30	210	30	84.63	6.16	7.32
40	38–11	50	4248	50	6557	50	28.8	50	16.360	50	224	50	155.68	11.39	9.52
	38–11 × WF9	50	4771	50	8036	50	37.4	50	20.730	50	248	50	177.10	13.10	10.49
	WF9 × 38–11	70	3947	70	7481	50	31.8	50	16.117	50	298	72	182.93	9.64	8.08
	WF9	50	4541	50	7121	50	32.4	50	16.050	50	290	50	173.20	10.05	8.48
60	38–11	50	4193	50	6973	50	36.0	50	19.264	50	224	50	210.7	13.84	8.37
	38–11 × WF9	50	4946	50	8441	50	50.0	50	27.152	50	256	50	260.0	16.34	9.45
	WF9 × 38–11	50	4322	50	7860	50	42.4	50	18.180	50	228	50	192.66	15.69	8.62
	WF9	50	4839	50	7575	50	44.0	50	17.570	50	220	50	184.86	16.67	8.68

[a] Symbols: W = Width in microns. L = Length in microns. V = Volume in mm³. Dw = Dry weight in mg. N = Number (Frequency). M = Mean.

[b] $\frac{A \times 100}{A + B}$ = Embryo in percentage of the embryo sac.

Series II, crosses between 38–11 and WF9 (pollinated on August 16, 1945).—The result of this repeated experiment shows the same initial development of the embryo in width (fig. 8). The hybrid WF9 and its maternal parent exceed the reciprocal hybrid 38–11 × WF9 and its maternal parent 38–11 for the period 12–16 days after pollination. Whether this is due to the different environmental conditions or due to the individual variation of the maternal plants is uncertain. For the period 16–21 days the growth rate of both inbred and hybrid embryos in width, as shown in fig. 8, agrees with the experiment in Series I. The sudden drop of the hybrid 38–11 × WF9 for the 25 days after pollination is apparently due to the individual variation of this particular parent plant, since it becomes the leading one again until maturity. At maturity the embryo width of hybrid 38–11 × WF9 remains at the top and that of inbred 38–11 at the bottom, while those of WF9 × 38–11 and inbred WF9 are found between.

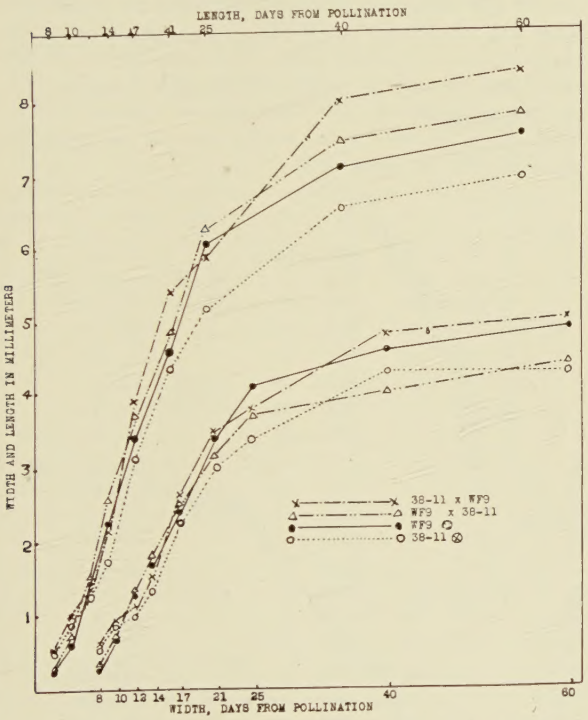
LENGTH, DAYS FROM POLLINATION
8 10 14 17 21 25 40 60
WIDTH AND LENGTH IN MILLIMETERS
1 2 3 4 5 6 7 8
38-11 x WF9
WF9 x 38-11
WF9 ♀
38-11 ♂
8 10 12 14 17 21 25 40 60
WIDTH, DAYS FROM POLLINATION

Fig. 8. Embryo development in width and length of selfed 38–11 and WF9 and their reciprocal hybrids.

The variability among the embryos appeared rather great in some samples of early collections. More advanced embryos showed greater uniformity in size. The standard error for each sample was not calculated. However, for the most variable sample tested, 8-day embryos of 38–11 and 38–11 × WF9, they were 508±7 and 544±11 microns in width respectively; the difference of 36 microns was found to be statistically significant, even though the length of the embryos was almost the same on 38–11 as on the maternal parent (table 1).

Series III, crosses between 38–11 and K–64 (pollinated on August 16, 1945).—The embryo width of the inbred 38–11 and of its hybrid 38–11 × K–64 exceeds that of the inbred K–64 and of its hybrid K–64 × 38–11, up to the time of 3 weeks after pollination (fig. 9). Both hybrids are above their respective maternal parents. Some changes take place during the next 3 weeks. The inbred 38–11 slows down and the inbred K–64 exceeds its hybrid, but is still next to the hybrid 38–11 × K–64 at the end of 40 days. At maturity, the inbred K–64 embryo is the widest, the hybrid 38–11 × K–64 is between the parents and the reciprocal hybrid K–64 × 38–11 embryo is just a little wider than that of inbred 38–11 (fig. 9).

In both cases, the crosses between 38–11 and WF9 and the crosses between 38–11 and K–64, the embryo width varies with the pure line and the kind of cross. At the first observation made 8 days after pollination, the embryo widths of three inbred lines differ in descending order as follows: 38–11, WF9, K–64. The growth rate in embryo width changes around the 3- and 6-week stages. The hybrid embryo is usually wider than that of its maternal parent with the exception of a cross K–64 × 38–11 in which the parent K–64 grows faster in width than the hybrid embryo growing on the same ear at the time of 3 weeks after pollination, as described above.

Embryo development in length.—Series I, crosses between 38–11 and WF9 (pollinated on August 12, 1945).—The mean embryo length of inbred 38–11 and of its hybrid 38–11 × WF9 is above that of inbred WF9 and of its hybrid WF9 × 38–11 at the 8-day stage. Two days later, however, the inbred 38–11 slows down in its growth rate in length and the hybrid WF9 × 38–11 exceeds both parents but it is still close to the hybrid 38–11 × WF9. This condition prevails until 25 days after pollination (table 1). Then the inbred WF9 comes to exceed the other inbred 38–11 in embryo length, though it is still below both hybrids toward the last observation, 44 days after pollination.

Series II, crosses between 38–11 and WF9 (pollinated on August 16, 1945).—The general tendency is the same as described in Series I, though the inbred line WF9 and hybrid WF9 × 38–11 reach a higher level during the period 12–25 days (fig. 8). The sudden drop of the embryo length of hybrid WF9 × 38–11 on the twenty-fifth day is possibly due to the general weakness of the particular plant. At maturity, both hybrids are greater in embryo length than the parents. Beginning 12 days after pollination, inbred WF9 remains above inbred 38–11 in embryo length throughout the series.

Series III, crosses between 38–11 and K–64 (pollinated on August 16, 1945).—In this experiment the difference of embryo length between hybrid 38–11 × WF9 and its maternal parent 38–11 and hybrid WF9 × 38–11 and its maternal parent WF9 is greater than that of the series I and II experi-

ments at 8 days (fig. 8 and 9). From 8 days on until maturity, hybrid 38–11 × K–64 maintains its leading position in embryo length all the way through, while parent K–64 is the slowest in growth of embryo length. The other hybrid exceeds both parents in embryo length only after 3 weeks following pollination. Parent 38–11 retains its position above parent K–64 until maturity, though it slows down in its embryonic growth rate in length after 25 days.

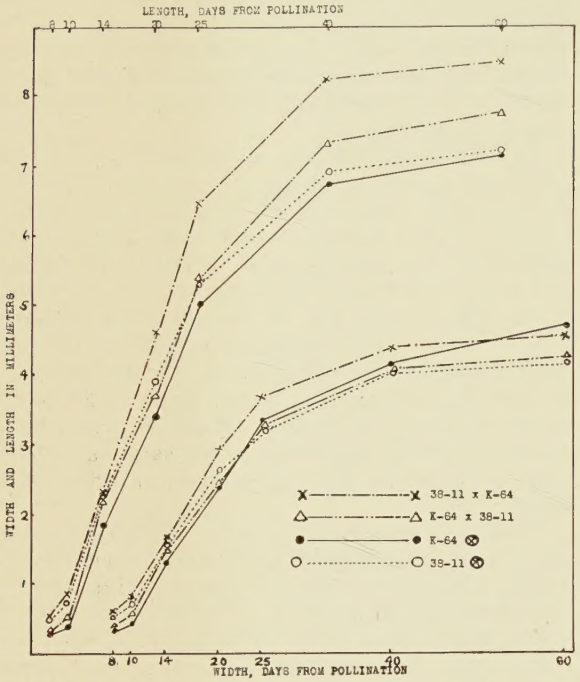

Fig. 9. Embryo development in width and length of selfed 38–11 and K–64 and their reciprocal hybrids.

In all cases studied the growth rate in length of the embryos of hybrids is greater than that of their maternal parents. Among three inbred lines studied it seems that the growth rate in length in K–64 is the slowest, in 38–11 it is the fastest, up to the stage of 10 days, when the embryo is highly active in differentiation. In WF9 it is slow in the early stage but faster in later stages. Just as in the case of growth in width, the growth in length changes during two periods: 8–14 and 20–25 days. Apparently the first change takes place during the morphological differentiation of different structures which involves orientation of the axis within the young embryo, while the second change takes place when the growth of the scutellum is mainly concerned.

Embryo development in volume.—Series I, crosses between 38–11 and WF9 (pollinated on August 12, 1945).—A study made by plotting the values for volume in table 1, showing the embryo development in volume for 16–44 days, indicates that the hybrid 38–11 × WF9 forges ahead throughout the whole period. The other hybrid WF9 × 38–11 is above both parents. In inbred WF9 the embryo development in volume is close to the other inbred 38–11 at first, but soon after 25 days, its growth rate by volume increases.

Series II, crosses between 38–11 and WF9 (pollinated on August 16, 1945).—During the early period, 12–15 days, the hybrid WF9 × 38–11 occupies the leading position in volume growth but soon the other hybrid 38–11 × WF9 takes its place (table 2). The inbred 38–11 remains at the lowest level in embryo volume. From 17 days on the two series generally agree except that the growth rate of the inbred increases a few days earlier. From 40 days to maturity, hybrid 38–11 × WF9 maintains its leading position in embryo development by volume. The inbred 38–11 is the slowest while the inbred WF9 is barely above the WF9 × 38–11 hybrid.

In comparison with the width and length of the embryo, the growth rate of inbred 38–11 is slower in width, in length and thickness than that of WF9 parent and the increase in volume of parent WF9 is chiefly attributed to the faster growth in thickness. The hybrid 38–11 × WF9 is the leading one in growth rate in volume and this is attributed to the thickness as well as width and length 2 weeks following pollination. The increase of volume in hybrid WF9 × 38–11 is mainly due to the greater growth rate in thickness.

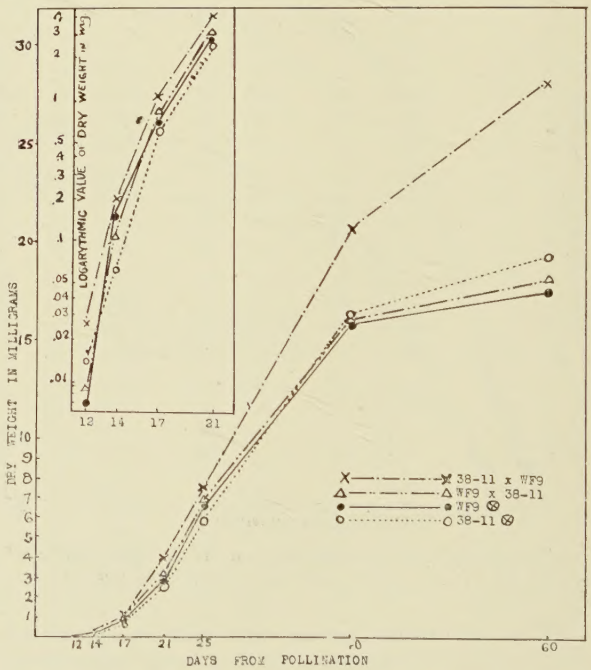

Fig. 10. Embryo development in dry weight of selfed 38–11 and WF9 and their reciprocal hybrids. The early stages are shown in logarithmic scale.

Series III, crosses between 38–11 and K–64 (pollinated on August 16, 1945).—The growth rate in volume of inbred 38–11 is much greater than that of K–64 during the early period of 14–20 days (table 3). It slows down somewhat after 25 days.

The embryo volume of hybrid 38–11 × K–64 maintains its superiority throughout the series. The inbred K–64 is retarded at first, but stands between 38–11 and the hybrid K–64 × 38–11 in embryo volume at maturity. The other hybrid K–64 × 38–11 follows the course of its maternal parent K–64 but is usually greater in volume.

Both hybrids are greater in volume than their respective maternal parents during development on the same ear. In comparison with the growth rate in width and in length, the main cause of increase in volume of hybrid 38–11 × K–64 at the later stages is attributed to the growth in thickness, while the growth rate in width is slow at that period.

Embryo development in dry weight.—Series I, crosses between 38–11 and WF9 (pollinated on August 12, 1945).—The growth rate in dry weight of hybrid 38–11 × WF9 is in the leading position throughout the observation during the period between 16 and 44 days (table 1). The other hybrid WF9 × 38–11 is above both parents up to the 20-day stage, but falls between the parents thereafter. The difference of dry weight between the two parents is slight.

Series II, crosses between 38–11 and WF9 (pollinated on August 16, 1945).—The inbred 38–11 embryo has about twice the dry weight as that of the other parent WF9 at the 8-day stage (fig. 10). Both hybrids are distinctly above their respective maternal parents. However, the lighter parent WF9 and its hybrid WF9 × 38–11 exceed the parent 38–11 and its hybrid 38–11 × WF9 on the same ear at the 14-day stage. Both slow down again afterwards (fig. 10). During the later stages the hybrid 38–11 × WF9 embryos are overwhelmingly superior to the reciprocal hybrid WF9 × 38–11 and both parents in dry weight, until maturity. The inbred 38–11 is a little above the inbred WF9 at later stages, with hybrid WF9 × 38–11 between both parents in dry weight.

In comparison with Series I of development in volume, it is of some interest to show here that the volume of parent 38–11 embryo and that of 38–11 × WF9 agree in giving more dry matter than the

TABLE 3. *Measurements of embryo and endosperm of 38–11 and K–64 and their reciprocal hybrids (pollinated on August 16, 1945).*

Days from pollination	Heritage	Measurements[a] Embryo (A) W N	W M	L N	L M	V N	V M	Dw N	Dw M	Endosperm (B) V N	V M	Dw N	Dw M	A × 100[b] / A + B V	A × 100[b] / A + B Dw
8	38–11	50	510	50	480	..	...	..	....	50	5.2	50	0.120	....	....
	38–11 × K–64	50	563	50	504	..	...	..	....	50	7.0	50	0.168	....	....
	K–64 × 38–11	50	367	50	328	..	...	..	....	50	5.0	50	0.130	....	....
	K–64	50	313	50	271	..	...	..	....	50	4.8	50	0.112	....	....
10	38–11	50	721	50	728	..	...	..	....	50	11.2	50	0.306	....	....
	38–11 × K–64	50	778	50	831	..	...	..	....	50	15.0	50	0.370	....	....
	K–64 × 38–11	50	558	50	519	..	...	..	....	50	10.8	50	0.252	....	....
	K–64	50	431	50	380	..	...	..	....	50	7.4	50	0.228	....	....
14	38–11	50	1783	50	2248	50	1.87	50	0.138	50	53.2	50	7.45	3.39	1.83
	38–11 × K–64	50	1610	50	2330	50	2.18	50	0.150	50	60.0	50	7.79	3.56	1.88
	K–64 × 38–11	50	1482	50	2194	50	1.30	50	0.122	50	73.0	50	8.25	1.88	1.46
	K–64	50	1315	50	1841	50	0.83	50	0.066	50	69.2	50	7.75	1.18	0.84
20	38–11	50	2641	50	3889	50	6.0	50	1.85	50	104	50	42.0	5.45	4.22
	38–11 × K–64	50	2906	50	4601	50	8.2	50	2.51	50	126	50	47.3	6.10	5.39
	K–64 × 38–11	58	2459	58	3693	50	4.4	50	1.57	50	116	50	43.7	3.65	3.47
	K–64	62	2398	62	3393	50	3.8	50	1.14	50	120	50	37.7	3.07	2.93
25	38–11	50	3237	50	5291	50	12.2	50	5.40	50	140	50	79.3	8.01	6.37
	38–11 × K–64	50	3692	50	6453	50	18.8	50	7.82	50	172	50	91.0	9.85	7.91
	K–64 × 38–11	124	3300	124	5387	50	13.6	50	5.54	50	158	50	89.4	7.92	5.83
	K–64	132	3341	132	5003	50	12.2	50	4.29	50	154	50	80.4	7.34	5.06
40	38–11	50	4063	50	6886	50	29.6	50	15.63	50	228	50	167.6	11.10	8.53
	38–11 × K–64	66	4385	66	8214	50	37.6	50	19.02	50	274	50	190.1	12.06	9.14
	K–64 × 38–11	50	4100	50	7305	50	26.8	50	14.49	50	210	50	162.6	11.31	8.24
	K–64	50	4155	50	6728	50	25.2	50	11.84	50	204	50	155.0	10.99	7.09
60	38–11	50	4244	50	7196	50	39.8	50	20.64	50	220	50	204.6	15.50	9.15
	38–11 × K–64	50	4559	50	8470	50	46.8	50	23.18	50	288	50	239.8	13.99	8.81
	K–64 × 38–11	50	4269	50	7730	50	41.0	50	19.61	50	220	50	205.3	15.70	8.68
	K–64	50	4717	50	7134	50	40.4	50	16.65	50	200	50	199.0	16.87	7.72

[a] Symbols: W = Width in microns. L = Length in microns. V = Volume in mm^3. Dw = Dry weight in mg. N = Number (Frequency). M = Mean.

[b] $\frac{A \times 100}{A + B}$ = Embryo in percentage of the embryo sac.

WF9 embryo and its WF9 × 38–11 hybrid embryo.

Series III, crosses between 38–11 and K–64 (pollinated on August 16, 1945).—The hybrid 38–11 × K–64 embryo maintains its leading position in dry weight throughout the series up to maturity (fig. 11). The inbred K–64 embryo remains at the lowest level throughout the entire period. The hybrid K–64 × 38–11 embryo comes close to the parent 38–11 in dry weight at 25 days, but soon drops again and is between both parents at maturity.

In comparison with embryo volume, it appears that the volume of 38–11 embryo and that of its hybrid 38–11 × WF9 contain more dry matter than those of parent K–64 embryo and its hybrid K–64 ×38–11 embryo.

Endosperm development of the inbred and hybrid maize.—Endosperm development in volume.—The tables include the data on the volumes of the endosperms. The young endosperm is soft, gelatinous and delicate. It shrinks considerably after fixation. However, no correction was made. Young endosperms shrink much more than the advanced ones. The variability is not great even in young stages, though no attempt was made to measure individual endosperms.

The results shown in the tables were plotted in graphs and diagrams, similar to those shown for dry weights, in fig. 12–14. For the graphs which are omitted here, the data are all included in the tables. The columns at the right, where the volumes of the embryos are expressed in percentages of the volumes of the embryo sac (100A/A+B), show the percentages for the endosperms when these values are subtracted from 100.

The volume of the endosperm will always show considerable shrinkage before maturity. Observations in series I were discontinued at about the stage when the volume of the endosperm has attained its maximum. After about 40 days it begins to shrink, whereas the dry weight continues to increase to maturity.

The analysis for progressive changes in endosperm volume shows that there appear to be significant differences at various stages of development between different inbred lines and the crosses made between them. Some endosperms grow relatively faster in early stages while others grow faster in later stages of development. Data such as these lend support to the thesis that different genes exert their influence at different times. As shown in the analysis for length and width of the embryo, which increase at different periods of development in various inbred lines, so also the endosperms of these lines appear to differ in their periods of maximum increase in volume.

Endosperm development in dry weight.—Series I, crosses between 38–11 and WF9 (pollinated on August 12, 1945).—The endosperm of inbred 38–11 is much heavier than that of inbred WF9 and the dry weights of the hybrid endosperms are nearly the same as their respective maternal parents at the first collection 8 days after pollination (table 1), but soon the hybrid endosperms gain weight at a faster rate throughout development. The inbred WF9 gains the least weight, while the hybrid 38–11 × WF9 maintains its leading position until the last observation, 44 days after pollination. The hybrid endosperm of WF9 × 38–11 exceeds both parents between 16 and 20 days and thereafter keeps close to the inbred 38–11. Inbred 38–11 exceeds inbred WF9 in dry weight throughout the whole period of observation.

Series II, crosses between 38–11 and WF9 (pollinated on August 16, 1945).—The endosperm of inbred 38–11 is more than twice the weight of that of inbred WF9. The endosperms of both hybrids are heavier than those of their respective maternal parents 8 days after pollination (fig. 12). This condition prevails up to 12 days. After 12 days the endosperm of hybrid WF9 × 38–11 exceeds in dry weight those of both parents as well as that of hybrid 38–11 × WF9, while the endosperm of inbred WF9 exceeds that of parent 38–11 and is close to that of hybrid 38–11 × WF9. This order continues until the 40-day collection. The hybrid WF9 × 38–11 and its maternal parent WF9 are much more vigorous in endosperm development than those found in series I. However, at maturity, the hybrid endosperm of 38–11 × WF9 gains the most in dry weight, its maternal parent is next, while inbred WF9 gains the least, with its hybrid WF9 × 38–11 slightly above.

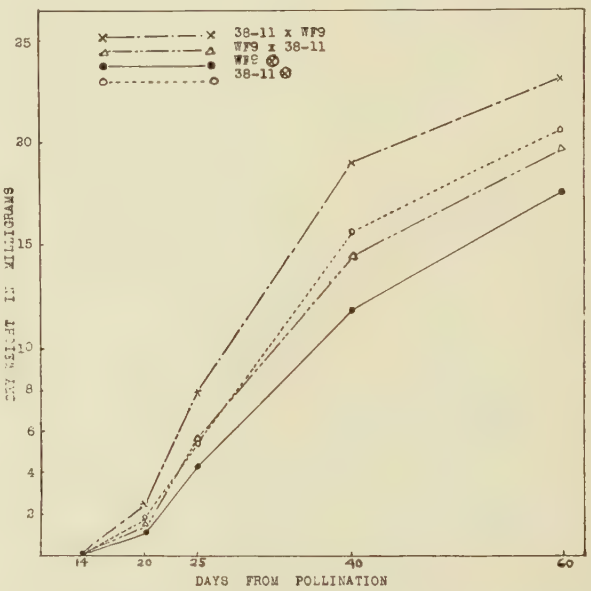

Fig. 11. Embryo development in dry weight of selfed 38–11 and K–64 and their reciprocal hybrids.

Series III, crosses between 38–11 and K–64 (pollinated on August 16, 1945).—The endosperm of inbred 38–11 is only a little heavier than that of inbred K–64 and the hybrids are much better than their respective maternal parents in the first ob-

servation at the 8-day stage (fig. 13). The hybrid 38–11 × K–64 gains the most in endosperm weight after 14 days. The endosperm of parent K–64 gains the least throughout development. The other parent gains more than K–64 in endosperm weight during the interval 25–40 days. The hybrid K–64 follows more or less inbred 38–11 in endosperm weight gains.

In the three series of experiments studied it seems that the hybrid endosperms gain more in dry weight than their respective maternal parents throughout the period of development. In the crosses of which the inbred line 38–11 is the maternal parent, the endosperm reaches the highest level in dry weight at maturity.

Relative development of embryo and endosperm in inbred and hybrid maize.—Relative development in dry weight.—Series I, crosses between 38–11 and WF9 (pollinated on August 12, 1945).—Table 1 shows for Series I the relative development of the embryo and endosperm in dry weight. In hybrid 38–11 × WF9 both the embryo and the endosperm gain in dry weight throughout development more than either of the parents or the other hybrid WF9 × 38–11. On the other hand, this hybrid embryo makes a particularly remarkable gain in relative weight after 20 days. In the reciprocal hybrid WF9 × 38–11 the embryo gains relatively more up to 20 days while the endosperm forges ahead rather late. In early stages, the endosperm of inbred 38–11 gains more in weight than that of inbred WF9; this difference diminishes with age.

Series II, crosses between 38–11 and WF9 (pollinated on August 16, 1945).—In hybrid 38–11 × WF9, the embryo gains rapidly in weight after 20 days, attaining its maximum relative weight in about 40 days, while the endosperm gains considerable weight after 40 days, with the result that it greatly exceeds endosperms of both parents and that of the reciprocal hybrid WF9 × 38–11 (fig. 14).

In inbred 38–11, the endosperm gains in weight rapidly in the later stages, especially before maturity, while the embryo gains somewhat in relative weight after 20 days.

In inbred WF9, the endosperm gains rapidly in the early stages and is retarded after 40 days; the embryo also gains weight faster in the early period, almost attaining its maximum relative weight at 40 days.

In hybrid WF9 × 38–11, the development in relative weight of embryo and endosperm follows more or less the course of the maternal parent WF9.

Series III, crosses between 38–11 and K–64 (pollinated on August 14, 1945).—In inbred K–64, the embryo gains slowly in weight throughout the development, attaining the maximum relative weight of only 7.72 per cent of the embryo sac, while the endosperm grows more rapidly in the period up to 25 days (fig. 14, right).

In hybrid K–64 × 38–11, the embryo gains relatively more weight in the early stages, and the endosperm forges ahead early too, with both values greater than those of the maternal parent K–64.

In hybrid 38–11 × K–64, the embryo gains rapidly in weight after the first observation at 14 days, attaining its maximum relative weight of 9.14 per cent at 40 days, while the endosperm exceeds endosperms of both parents and hybrid K–64 × 38–11 after 20 days and also gains considerable weight just before maturity.

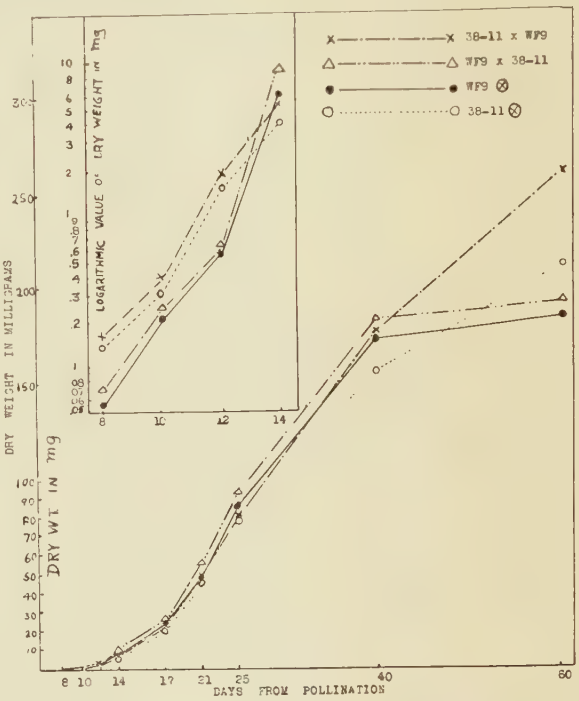

Fig. 12. Endosperm development in dry weight of selfed 38–11 and WF9 and their reciprocal hybrids. The early stages are shown in logarithmic scale.

In parent 38–11 the embryo begins to gain weight about 20 days after pollination, attaining the maximum relative weight of 9.15 per cent at maturity, while the endosperm gains its weight somewhat less rapidly in the later stages.

Relative development of embryo and endosperm in volume.—Series I, crosses between 38–11 and WF9 (pollinated on August 12, 1945), and II, crosses between 38–11 and WF9 (pollinated on August 16, 1915).—The relative development of embryo and endosperm in volume is shown for Series I and II in tables 1 and 2.

In inbred 38–11 the endosperm grows rather less in volume during the early stages up to 25 days after pollination and reaches the level of inbred WF9 between 25–44 days, while the embryo grows more in volume in the early stages before 20 days and is somewhat retarded through the period 25–44 days.

In inbred WF9 the endosperm grows faster in the early stages while the embryo forges ahead after 20 days following pollination with the result that

it attains more than 15 per cent in volume of the embryo sac toward the observation 44 days after pollination.

In hybrid 38–11 × WF9 the relatively rapid early growth of the embryo is combined with the overwhelming growth in volume of the endosperm between the period 25–44 days, with both values exceeding those of both parents and the reciprocal hybrid.

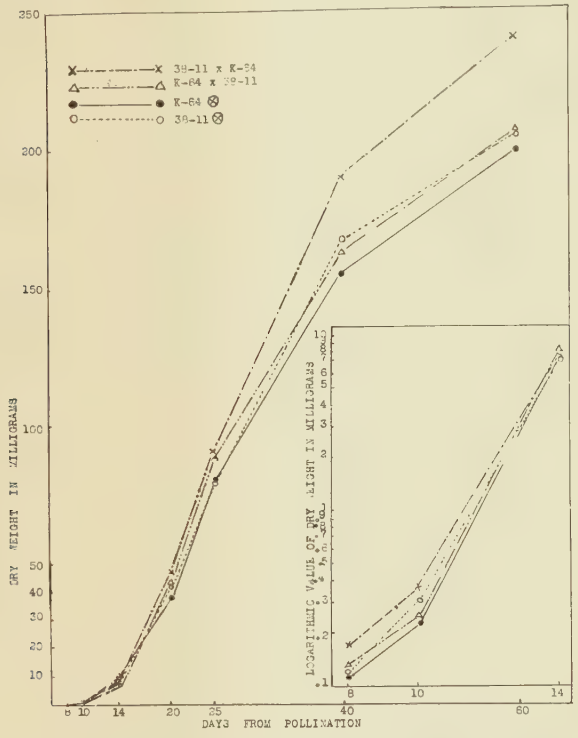

Fig. 13. Endosperm development in dry weight of selfed 38–11 and K–64 and their reciprocal hybrids. The early stages are shown in logarithmic scale.

In the hybrid WF9 × 38–11 the embryo grows relatively more in the early stages and slows down somewhat in later stages, while the endosperm exceeds those of both parents.

Series III, crosses between 38–11 and K–64 (pollinated on August 16, 1945).—Table 3 shows the relative development for Series III of embryo and endosperm.

In inbred K–64 the endosperm forges ahead early and is always larger than in inbred 38–11, while the embryo begins to gain in volume after 20 days and makes considerable growth even after 40 days.

In inbred 38–11 the endosperm is more or less retarded and forges ahead rather late in comparison with that in K–64, while the embryo of 38–11 forges ahead early, attaining nearly half of its relative volume in 20 days.

In hybrid 38–11 × K–64 the relative early growth of the embryo is combined with rapid total growth of the endosperm, with both of their values reaching the maximum only near the end of the growing period.

The hybrid K–64 × 38–11 with rapid growth of the endosperm in the early stage and the later gain in volume of the embryo follows rather closely the maternal course of development.

From the studies of the relative development of the embryo and endosperm in volume, in the three preceding series, two points may be generalized as follows: (1) The hybrid embryos gain their greater relative volume in all of the stages before maturity in comparison with embryos of their respective maternal parents. However, this difference results in the reverse order at maturity with the exception of the 38–11 × WF9 hybrid. (2) The pollen of WF9 or K–64 seems to be more effective when either of their single set of chromosomes is added to the endosperm of 38–11 than the pollen of 38–11 when its nuclear contribution is added to the endosperm of WF9 or K–64.

Discussion.—*Seed and embryo size factors in relation to heterosis.*—Embryo and endosperm are two main parts within a seed. Genetically the embryo is diploid while the endosperm is triploid. Since the triploid endosperm receives double sets of chromosomes from the maternal parent, the latter exerts more control over kernel size. The embryo and endosperm maintain a degree of equilibrium during their development. Besides, the limitation of the pericarp may also be an important controlling factor in seed size. If the larger hybrid embryo has a larger endosperm as well, it has an advantage after germination. However, as Sprague (1936) and Kempton and McLane (1942) concluded, heterosis is not necessarily reflected in embryo size. Collins (Richey, 1935) also found that the large hybrid seeds of maize showed a significantly higher growth rate only for about 2 weeks. The initial advantage of the larger seed or embryo size is, as Whaley (1944) summarized, "usually lost before maturity is reached."

Table 4 shows the increase by dry weight of embryo and endosperm of both reciprocal hybrids in percentage of those of the maternal parent from the same ear. In cross 38–11 × WF9 it is evident that hybrid vigor in the embryo attains its maximum during differentiation and soon after between 12 and 17 days, while that of the endosperm also attains its maximum in the early stages around 10 to 17 days. In the reciprocal cross WF9 × 38–11, the hybrid embryo gains most extraordinarily during the period from 12 to 17 days, but the relative vigor almost disappears toward maturity. The endosperm of this hybrid also gains much more in the early stages between 14–16 days and this gain diminishes with age. In the cross 38–11 × K–64, the embryo is the most vigorous at 25 days; on the other hand, the endosperm shows its relative maximum at 8 days. In the reciprocal cross K–64 × 38–11 the vigor of the embryo manifests its remarkable gain in about 14 days and decreases with age, while the endosperm shows relatively low vigor, diminishing

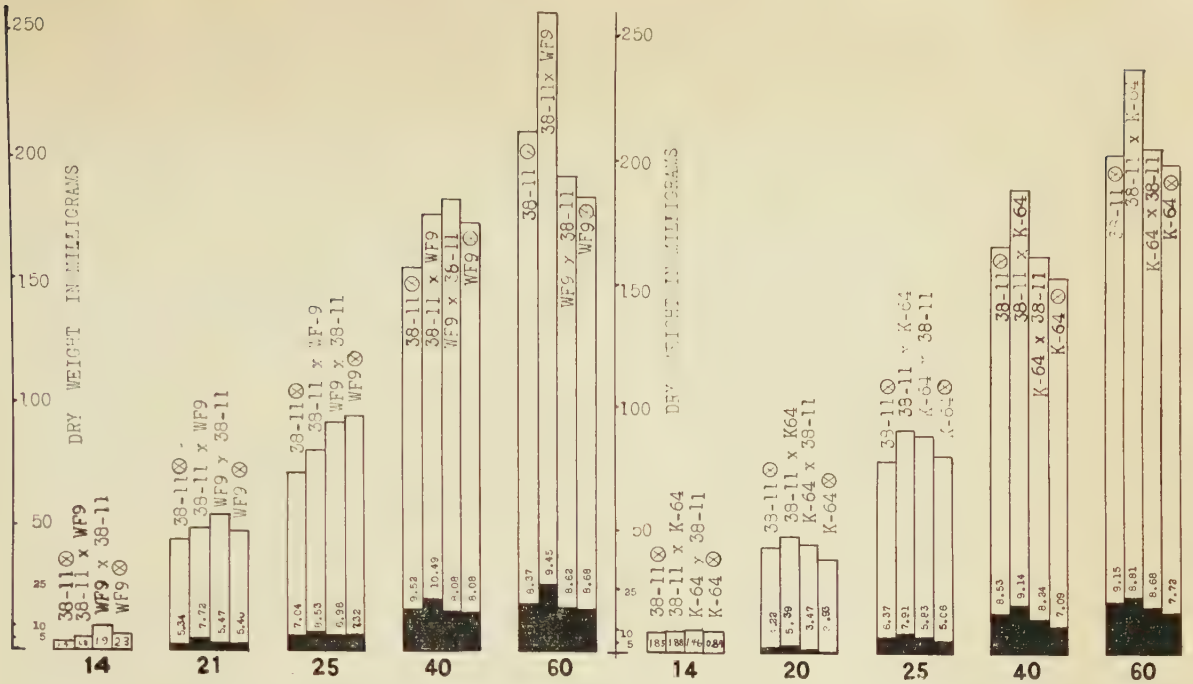

Fig. 14. Relative development in dry weight of selfed 38–11 and WF9 and their reciprocal hybrids (left) and selfed 38–11 and K–64 and their reciprocal hybrids (right). The total length of the column represents the endosperm dry weight and its solid portion represents the embryo dry weight. The figure inside the column indicates the percentage of embryo in total weight of endosperm and embryo combined.

toward the end. If heterosis means that the hybrid exceeds both parents, it is evident that hybrid vigor of the mature embryo and endosperm shows only in the cross of which the inbred line 38–11 is the maternal parent. In the reciprocal cross of which either the inbred line WF9 or K–64 is the maternal parent, the results in both hybrid embryo and endosperm are much larger than those of the maternal parent on the same ear. They only approach and do not exceed those of the pollen parent.

The difference of the embryo and endosperm between the inbred and hybrid is the result of the

TABLE 4. *Comparison of gain by weight of embryo and endosperm in reciprocal hybrids, in per cent of those of maternal parent taken from same ear.*

Days from pollination	8	10	12	14	16	17	20	21	25	40	44	60
Series I												
38–11 × WF9												
Embryo	...	...	...	...	127.2	...	69.5	...	46.4	...	39.6	...
Endosperm	21.4	33	13.1	...	32.2	...	14.4	...	11.3	...	19.8	...
WF9 × 38–11												
Embryo	...	...	...	...	84.6	...	22.9	...	15.8	...	—2.2	...
Endosperm	0	17.3	1.7	...	57	...	19.8	...	20.1	...	7.9	...
Series II												
38–11 × WF9												
Embryo	...	...	85.8	71	...	74.5	...	61.6	28.2	26.7	...	40.9
Endosperm	19.1	28.2	25.6	33.2	...	29.2	...	8.7	4	13.8	...	23.4
WF9 × 38–11												
Embryo	...	...	28.2	31.3	...	23 6	...	17.4	3.7	0.4	...	3.5
Endosperm	30.4	20.2	14.5	54.4	...	38	...	15.9	9.6	5.6	...	4.2
S ries III												
38–11 × K–64												
Embryo	...	...	...	8.7	...	...	35.7	...	44.8	21.7	...	12.3
Endosperm	40	20.9	...	4.6	...	...	12.6	...	14.8	13.4	...	17.2
K–64 × 38–11												
Embryo	...	...	...	84.9	...	...	37.7	...	29.2	21.5	...	17.8
Endosperm	16.1	10.5	...	6.5	...	...	15.9	...	11.2	4.9	...	3.7

difference in growth rate during development between the hybrid and the parent as analyzed in this investigation. The difference is greater in early stages. The fact that the hybrid maize has a greater embryo is not the cause of hybrid vigor as Ashby interpreted. The "initial capital" of the plant is the fertilized egg. Since a hybrid zygote is no larger than that of a selfed zygote, the early greater difference of embryo size in favor of the hybrid appears to result from the rapid growth rate after the zygote has become multicellular. Furthermore, the difference is not maintained but decreases or disappears before the maturity of the embryo. It is obvious that the growth rate changes at different stages during embryological development.

Embryological studies of hybrid vigor.—Since the hybrid seeds are growing on the same ear with those of the maternal parent, the environmental factor of variation is equalized in the present investigation. However, the pollen parent is still subjected to variations in the environment and the variation of the individual plant. From the studies of the growth curves we may conclude that the hybrid embryo and hybrid endosperm always exceed the embryo and endosperm of the maternal parent in all measurements save width.

It appears probable that a number of genes are responsible for different phases in growth. It seems that some genes affect the early part of the embryology, while others affect the later part of the development. As described above embryological development may be divided into different morphological stages. If different stages are controlled by different genes or groups of genes, some of the growth factors or genes could be detected only through embryological studies.

The results of these investigations are of some interest in connection with the explanation of the nature of hybrid vigor. On the assumption that genes or groups of genes have a specific time of action during different phases of embryological development, the higher growth rate of the vigorous hybrid would be attributed to the interaction of genes or groups of genes which control the physiological processes. Hybrid vigor does not necessarily mean that the hybrid embryo exceeds its parents in every respect, but rather that the combined effect of all the factors produces a larger embryo. This is illustrated in the cross between the pure lines 38–11 and K–64 (table 3). Here the mature embryo of the hybrid greatly exceeds the mature embryos of both parents in length, in volume and in dry weight, while so far as its width is concerned, it is between the parents.

The mechanism of heterosis, as expressed in hybrid vigor, is still unknown. Since the difference of the growth rate between the hybrid and the inbred is present in the early embryological stages, it is desirable to know more about gene action during development. Heterosis is caused by the combined effects of genes or groups of genes on the physiological processes, by means of complementary, cumulative, or duplicate gene actions. The results of the present investigation favor this explanation rather than one based upon a single gene as Ashby suggested.

SUMMARY

Embryological development of maize between fertilization and maturity of the kernel was studied by growing the hybrids on the same ears with the maternal parents. The relative rate of growth in comparison with its endosperm was described for inbreds and their reciprocal hybrids at various periods of development. The growth rate of the embryo as represented in width, length, volume and dry weight varies with different lines and many of these differences are already apparent 8 days after pollination. Generally the hybrid embryos and endosperms are larger than those of the maternal parents. The differences are greatest in the early stages. The growth rates of embryo and endosperm change during development. The larger size of hybrid maize kernels is the result of differences in growth rate during development. "Initial capital" is not the cause of hybrid vigor. It is suggested that hybrid vigor during the maturity of the kernel is determined by genes or groups of genes which act at different stages during embryological development.

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VITA

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1. S. W. Loo and F. H. Wang, 1943. The culture of young conifer embryos in vitro. Science 98: 544.
2. Wang, F. H., 1944. The life history of *Keteleeria*. (An Abstract.) Amer. Jour. Bot. 31: 6s.